

# Role of Oviposition Preference in an Invasive Crambid Impacting Two Gramineaceous Host Crops

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**ABSTRACT** Oviposition preference studies of the Mexican rice borer, *Eoreuma loftini* (Dyar), on sugarcane, *Saccharum* spp., and rice, *Oryza sativa* L., showed that drought stressed sugarcane was 1.8-fold more attractive based on egg masses/plant than well watered sugarcane. The *E. loftini* susceptible sugarcane cultivar LCP 85–384 was 1.6-fold more attractive than HoCP 85–845 based on numbers of eggs per egg mass. Egg masses were 9.2-fold more abundant and 2.3-fold larger on sugarcane than on rice. Rice, however, was preferred to sugarcane on a plant biomass basis. Oviposition on sugarcane occurred exclusively on dry leaf material, which increased under drought stress. Egg masses per plant increased on drought stressed sugarcane and were correlated with several foliar free amino acids essential for insect growth and development. The more resistant (based on injury) but more attractive (based on oviposition) rice cultivar XL8 had higher levels of several free amino acids than the susceptible cultivar Cocodrie. The association of host plant characteristics to oviposition preference is discussed. Projected oviposition patterns relative to sugarcane and rice production areas were estimated for Texas and Louisiana based on the availability of each host in different regions of each state. These results suggest that, where sugarcane and rice co-occur, the majority of eggs would be found on sugarcane early in the season, because of this crop's substantially greater biomass compared with rice. Abundance later in the season would also favor sugarcane; however, the abundance on rice would be greater than expected solely based on host availability, largely because of the greater preference per gram of rice plant dry weight.

**KEY WORDS** Mexican rice borer, *Eoreuma loftini*, sugarcane, rice, oviposition

Oviposition of many lepidopterans is a critical step in their life cycles because of the limited mobility of first instars (Feeny et al. 1983, Showler 2002, Showler and Moran 2003). Visual, olfactory, gustatory, and mechanical senses are used by ovipositing females in host plant selection (Ramaswamy 1988). Plant phenotypic characters that influence acceptability for insect oviposition include leaf pubescence (Sosa 1988), color (Levinson et al. 2003), phenological stage (Moré et al. 2003), and leaf shape (Mackay and Jones 1989). In addition, stress (Showler and Moran 2003), nutritional status (Myers 1985, Showler and Moran 2003), and secondary metabolites (Feeny et al. 1983) influence host selection by insect herbivores. Determining causal factors underlying pest oviposition patterns and

quantifying oviposition preference for host crops can assist in the development of pest management strategies (Renwick and Chew 1994, Showler 2004a).

The availability of host plant free amino acids (FAAs) is a critical factor in population growth of many insect herbivores (McNeil and Southwood 1978), and insects can respond to changes in the nutritional quality of a plant (Rhoades 1983, Showler 2004a, Showler and Robinson 2005). Accumulations of host plant FAAs have been associated in many plants with numerous stresses (Rabe 1994, Showler 2004b), including drought (Gzik 1996, Showler 2002). Accumulated FAAs lower the water potential of cells and may reduce water loss through osmoregulation (Heuer 1994).

The Mexican rice borer, *Eoreuma loftini* (Dyar), is known to feed on >15 plant species in North America (Reay-Jones 2005), including the crop plants corn, *Zea mays* L., sorghum, *Sorghum bicolor* L. Moench (Youn et al. 1988), rice, *Oryza sativa* L. (Reay-Jones et al. 2005b), and sugarcane, *Saccharum* spp. (Meagher et al. 1994). *Eoreuma loftini* originated in Mexico and became the dominant insect pest of sugarcane in the Lower Rio Grande Valley of Texas since it became established in 1980 (Johnson 1984), now representing >95% of the sugarcane stalk borer population, which

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Table 1. Design of *E. loftini* oviposition studies, Weslaco, TX, 2003–2004

Species	Cultivar	Stage	Stress (sugarcane only)	Dataset						
				1	2	3	4	5	6	7
Sugarcane	LCP 85–384	5 nodes	Non-drought stressed	X						
			Drought stressed	X	X					
	HoCP 85–845	10 nodes	Non-drought stressed						X	X
			Drought stressed							X
		5 nodes	Non-drought stressed	X	X					
			Drought stressed	X						
Rice	Cocodrie	10 nodes	Non-drought stressed							X
			Drought stressed						X	X
		Tillering 5–6 nodes					X			
		Tillering 9–11 nodes				X	X	X		
	XL8	Boot			X	X				
		Heading						X	X	
		Tillering 5–6 nodes					X			
		Tillering 9–11 nodes				X	X	X		
		Boot			X	X				
		Heading						X	X	

consists of *E. loftini* and the sugarcane borer, *Diatraea saccharalis* (F.) (Legaspi et al. 1999b). By 1989, it moved into the rice production area of east Texas (Browning et al. 1989), where it is responsible for major yield loss in rice (Reay-Jones et al. 2005b). Invasion of Western Louisiana, where sugarcane and rice are grown in close proximity, is likely imminent (Reay-Jones et al. 2007). The objectives of this study were (1) to quantify *E. loftini* oviposition on sugarcane and rice cultivars at different phenological stages, (2) to identify selected potential biochemical mechanisms behind these relationships, and (3) to estimate oviposition patterns on sugarcane and rice in Texas and projected patterns in Louisiana.

### Materials and Methods

This study was conducted at the Texas A&M Agricultural Experiment Station in Weslaco, TX, during the summers of 2003 and 2004. Sugarcane plants (cultivars LCP 85–384 and HoCP 85–845) were grown in a greenhouse in 3.8-liter pots containing nursery potting soil (Metromix 300; Sun Gro Horticulture Canada, Seba Beach, Canada). Sugarcane nodes collected in fields in the Lower Rio Grande Valley of Texas were planted individually in pots and fertilized with 200 ml of Peters Professional water-soluble general purpose 20-20-20 N-P-K (Scotts-Sierra Horticultural Products, Maryville, OH) at 18.3 g/liter of water approximately once every 4 wk. Plants were watered with 1.5 liters three times per week. The two phenological stages of sugarcane used in this study were plants with five elongated nodes ( $\approx 89$  cm from soil surface to plant apex of the stalk) and elongated 10 nodes ( $\approx 158$  cm from soil to apex of the stalk). In the drought-stressed treatment, sugarcane plants were watered once a week with 1.5 liters for 2 wk before starting the experiments, whereas the nonstressed controls stayed on the normal irrigation regimen. The watering treatments were initiated before the plants reached the 5- and 10-node stages.

Rice cultivars Cocodrie and XL8 were grown in the greenhouse in 1.1 liter of potted soil (3 plants/pot),

and received two applications of 0.79 g/pot of urea (46% N) corresponding to 207 kg/ha of N at 1 and 5 wk after emergence. Rice was flooded 6 wk after emergence. The four phenological stages used in this study were the 5–6 node tillering (1 wk after emergence), 9–11 node tillering (3 wk after emergence), boot (7 wk after emergence), and full panicle exertion (10–11 wk after emergence) (Vergara 1991).

**Oviposition Choice Tests.** *Eoreuma loftini* adults were obtained from a laboratory colony at the Texas A&M System Agricultural Research and Extension Center in Weslaco that was initiated from larvae collected in sugarcane fields in the Lower Rio Grande Valley of Texas. Every year, field-collected larvae were added to the colony. The insects were reared on artificial diet in an environmental chamber (Martinez et al. 1988) at 25°C, 65% RH, and a photoperiod of 14:10 (L:D). Pupae were separated by sex and placed in 3.8-liter plastic containers for emergence under the same conditions. Adults used in these experiments were 48 h old.

Seven oviposition experiments were conducted, with four treatments in each, covering the 16 treatments described in Table 1. Each experiment had either sugarcane (1 and 7), rice (3–5), or sugarcane and rice (2 and 6). Each test was a randomized complete block design (four blocks) with two plants (subsamples) of each of the four treatments within each block. A greenhouse cage (2 by 2 by 2 m) was used as a block, with the eight pots randomly placed on a 1.5-m circle in the center of each cage. Each experiment was initiated with the release of 30 male and 30 female moths in each cage and ended 6 d later. Numbers of eggs and egg masses and location of the eggs on the host plant were recorded. For the remainder of this paper, data from an experiment are referred to as datasets 1–7 (as depicted in Table 1).

**Plant Measurements.** At the end of each experiment, elongated nodes, and green and dry leaves were counted on each sugarcane plant. Rice tillers and green and dry leaves were counted. Dry weight was determined for plants in three pots of each treatment after 5 d in an oven at 75°C. Weights on a per plant

Table 2. Sugarcane and rice measurements from greenhouse oviposition test, Weslaco, TX, 2003–2004

Species	Cultivar	Stage	Stress (sugarcane only)	Weight per plant (g)	Leaves per plant	Dry leaves per plant	Water potential (sugarcane) [bar]	Tillers per plant (rice)	
Sugarcane	LCP 85–384	5 nodes	No	50.8b	17.2abc	7.2cd	8.7c	—	
			Yes	26.9c	16.9bc	10.6b	29.3a	—	
	HoCP 85–845	10 nodes	No	104.7a	19.2ab	9.2bc	10.7bc	—	
			Yes	102.0a	21.0a	14.4a	26.4a	—	
		5 nodes	No	43.2b	15.0cd	5.2d	8.1c	—	
			Yes	16.8cd	14.6cd	8.9bc	23.0ab	—	
		10 nodes	No	104.2a	19.6ab	7.2cd	13.5bc	—	
			Yes	99.3a	19.7ab	9.7bc	11.5bc	—	
Rice	Cocodrie	Tillering 5–6 nodes	—	0.12e	4.0hi	0.0e	—	1.0d	
		Tillering 9–11 nodes	—	0.60e	7.7gh	0.7e	—	1.6cd	
		Boot	—	1.57e	9.9fg	1.2e	—	1.7cd	
		Heading	—	3.96de	10.6ef	1.9e	—	2.0bc	
	XL8	Tillering 5–6 nodes	—	0.05e	4.6hi	0.04e	—	1.5cd	
		Tillering 9–11 nodes	—	0.76e	10.6ef	0.5e	—	2.6ab	
		Boot	—	1.92e	14.0cd	1.5e	—	3.1a	
		Heading	—	5.54de	13.3de	1.7e	—	2.5ab	
		<i>F</i>			320.29 <sup>a</sup>	55.34 <sup>b</sup>	66.95 <sup>b</sup>	9.67 <sup>c</sup>	14.73 <sup>d</sup>
		<i>P</i> > <i>F</i>			<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Means within the same column followed by the same letter are not significantly different ( $P < 0.05$ ; Tukey's [1953] HSD).

<sup>a</sup> df = 15,68; <sup>b</sup> df = 15,96; <sup>c</sup> df = 7,24; <sup>d</sup> df = 7,56.

basis are presented in Table 2. In experiments 1 and 3 (Table 1), the third leaf from the apex of each sugarcane plant ( $n = 8$  per treatment) was excised, and water potential was measured immediately with a model 610 (PMS Instrument Co., Corvallis, OR) pressure bomb at 0900 hours. The second leaf from the apex of the plant was excised and placed on dry ice for all sugarcane treatments in experiments 1 and 7 and for rice treatments in experiments 2 and 6 ( $n = 8$  per treatment). Each 1-g leaf tissue sample was homogenized with 10 ml of 0.1 N HCl using a Virtishear homogenizer (Virtis, Gardiner, NY). Five grams of homogenate from each sample was placed in separate 10-ml tubes and centrifuged at 10,000 rpm for 30 min. Samples were stored at  $-80^{\circ}\text{C}$ .

One milliliter of supernatant from each sample was filtered through a 0.5- $\mu\text{m}$  filter (Econofilter; Agilent, Santa Clara, CA; pore size = 0.45  $\mu\text{m}$ , diameter = 25 mm) fitted to a 5-ml plastic syringe. Samples were placed in the autosampler of an Agilent 1100 Series (Agilent Technologies, Atlanta, GA) reversed-phase high-performance liquid chromatograph (HPLC) with a binary pump delivering solvent A (1.36 g sodium acetate trihydrate + 500 ml purified HPLC grade water + 90  $\mu\text{l}$  triethylamine [TEA] + sufficient acetic acid to bring the pH to  $7.2 \pm 0.05$  [95% CI]) and solvent B (1.36 g sodium acetate trihydrate + 100 ml purified HPLC grade water [acetic acid added to this mixture to bring the pH to  $7.2 \pm 0.05$ ; 95% CI] + 200 ml acetonitrile + 200 ml methanol) at 100 and 1.0 ml/min on a Zorbax Eclipse AAA 4.6 by a 150-mm 3.5- $\mu\text{m}$  column (Agilent Technologies). Absorbances at 262 and 338 nm were monitored on a variable wavelength detector for 48 min/sample. The autosampler measured and mixed 6  $\mu\text{l}$  sodium borate buffer (0.4 N, pH 10.2 in water), 1  $\mu\text{l}$  9-fluorenylmethylchloroformate (FMOC), and 1  $\mu\text{l}$  ophthalaldehyde (OPA) derivitizing agents, and 2  $\mu\text{l}$  of sample, and then injected 2  $\mu\text{l}$  for chromatographic separation of free amino

acids (FAAs). Identification and quantification of 17 derivitized FAAs (alanine, arginine, aspartic acid, cysteine, glutamic acid, glycine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, proline, serine, threonine, tyrosine, and valine) were achieved by calibrating with a standard mixture of amino acids. Peak integration accuracy was enhanced by manual establishment of peak baselines using Agilent software.

**Data Analyses.** Oviposition choice, based on egg masses, eggs per egg mass and total eggs per plant, were analyzed for significant departure from randomness by performing  $\chi^2$  analyses of contingency tables (Zar 1999) for each dataset and overall for the entire experiment. Expected frequencies of egg laying for each of the four treatments in each dataset were one-fourth, one-fourth, one-fourth, and one-fourth, which would occur if oviposition choice was random.

Preference can be quantified as departure from the probability of randomly selecting a host based on availability and has been used to predict patterns of herbivore oviposition, parasitism, and predation on different hosts (Murdoch 1969, Manly et al. 1972, Chesson 1978, Wilson and Gutierrez 1980, Pickett et al. 1989, Murphy et al. 1991). When multiple hosts are simultaneously made available to an herbivore, preference coefficients on either a per plant or a per gram host dry mass basis can be derived using equation 1.

$$\hat{\alpha}_{ij} = \frac{n_{ij}}{\max n_j} \quad [1]$$

where  $\hat{\alpha}_{ij}$  = estimated preference shown for the  $i$ th host for the  $j$ th dataset;  $n_{ij}$  = mean number of eggs laid per plant or per gram of plant dry mass, respectively, on the  $i$ th treatment for the  $j$ th dataset; and  $\max n_j$  = mean maximum number of eggs laid per plant or per gram of plant dry mass respectively, across treatments for the  $j$ th dataset.

When combined with estimates of the relative density (i.e., plants per pot: one for sugarcane, three for rice) or mass of each host for a particular dataset, preference coefficients can in turn be used to provide estimates of relative host selection for each host type (equation 2).

$$\hat{n}_{ij} = n_j \hat{\alpha}_{ij} A_i / \sum_{i=1}^i \hat{\alpha}_{ij} A_i \quad [2]$$

where  $\hat{\alpha}_{ij}$  = the estimated relative preference shown for the  $i$ th host for the  $j$ th dataset;  $\hat{n}_{ij}$  = the estimated number of eggs, egg masses, or eggs/egg mass oviposited on the  $i$ th host; and  $A_i$  = relative density or mass of the  $i$ th host.

Although equation 1 is extremely easy to use, preference coefficients derived from separate experiments or datasets can only be compared if they share two or more common hosts; otherwise, the values of different sets of coefficients are not relative to each other. In our experiment, two treatments overlap between each successive dataset, thereby providing common hosts. Experiment-wide estimates of each preference coefficient can be derived from the data using iterative nonlinear least squares regression based on the modified Gauss-Newton method (JMP; SAS Institute 2002) (equation 3).

$$D_n = \sum_{j=1}^7 \sum_{i=1}^k (n_{ij} - n_j \alpha_i A_i / \sum_{i=1}^i \alpha_i A_i)^2 \quad [3]$$

where  $D_n$  = the minimized deviation of observed from predicted number of eggs, egg masses, or eggs per egg mass.

Once the experiment-wide estimates are derived, least squares estimates of preference coefficients for each of the individual datasets can in turn be derived by minimizing the deviation between the experiment-wide estimates ( $\alpha_i$ ) and the iteratively scaled preliminary estimates ( $[\text{carot}] \alpha_{ij}$ ) obtained from equation 1 (see equations 4 and 5 using equation 6).

$$D_\alpha = \sum_{j=1}^7 \sum_{i=1}^k (\hat{\alpha}_{ij} \beta_j - \alpha_i)^2 \quad [4]$$

$$\alpha_{ij} = \hat{\alpha}_{ij} \beta_j \quad [5]$$

$$D_{\alpha,j} = \sum_{i=1}^k (\hat{\alpha}_{ij} \beta_j - \alpha_i)^2 \quad [6]$$

where  $D_\alpha$  = the minimized deviation of observed from predicted preference estimates across all hosts  $i$  and all datasets  $j$ ;  $\alpha_{ij}$  = the individual experiment based preference estimates shown for the  $i$ th host for the  $j$ th dataset; and  $D_{\alpha,j}$  = the minimized deviation of observed from predicted preference estimates for each dataset  $j$  across all hosts  $i$ .

The effect of plant characteristics on the preference coefficients ( $\alpha_{ij}$ ) derived for each dataset was estimated using multiple linear regression analysis (PROC REG; SAS Institute 1999). The number of dry

leaves per plant was included in the model for sugarcane based on previous research (Van Leerdam et al. 1986) showing the importance of this variable for *E. loftini* oviposition behavior. Preference coefficients  $\alpha_{ij}$  were used to establish Pearson correlations with plant measurements (PROC CORR; SAS Institute 1999). Plant measurements were pooled across experiments and analyzed with a one-way analysis of variance (ANOVA; PROC MIXED; SAS Institute 1999), and Tukey's honestly significant difference (HSD) (Tukey 1953) was used for mean separation. Means were compared using contrasts ( $\alpha = 0.05$ ) and family-wise error rates were corrected using the stepdown method (PROC MULTTEST; SAS Institute 1999).

Simulated oviposition patterns on sugarcane and rice were predicted in four geographical regions: (1) Texas rice belt west of Houston (Austin, Brazoria, Calhoun, CO, Fort Bend, Galveston, Harris, Jackson, Matagorda, Victoria, Waller, and Wharton counties), (2) Texas rice belt east of Houston (Chambers, Jefferson, Liberty, and Orange counties), (3) southwest Louisiana (Acadia, Allen, Avoyelles, Beauregard, Calcasieu, Cameron, Evangeline, Jefferson Davis, Lafayette, Pointe Coupee, Rapides, and Vermilion parishes), and (4) southcentral Louisiana (Assumption, Ascension, East Baton Rouge, Iberia, Iberville, Lafourche, St. Charles, St. James, St. John the Baptist, St. Martin, St. Mary, Terrebonne, and West Baton Rouge parishes). For each region, the relative amount of oviposition on sugarcane and rice was predicted for each of four dates (1 May, 15 May, 15 June, and 6 July), corresponding to the four rice growth stages in our preference experiments. Projected oviposition patterns were estimated using equation 1, with the experiment-wide preference coefficients based on *E. loftini* eggs per gram of dry weight, and host availability based on estimated sugarcane and rice plant dry weight in each region on each date. Preference estimates for the nondrought stressed sugarcane cultivar LCP 85-384, the dominant sugarcane cultivar in Louisiana (Legendre and Gravois 2005), and the rice cultivar Cocodrie, the dominant rice cultivar in Texas and Louisiana, were used in the analysis. Because preference was only measured for two sugarcane growth stages, the youngest of which corresponded to the oldest rice growth stage, we approximated the preference for sugarcane at three of the four dates by linear extrapolation. The 5- and 10-node sugarcane stages corresponded to  $\approx 6$  July and 10 August, respectively. In the four regions, the area producing sugarcane (Legendre and Gravois 2005) and rice (Texas A&M University System Agricultural Research and Extension Center in Beaumont) were estimated. Plant weight in each region for each of the four dates was calculated by multiplying production area by estimated biomass per hectare for sugarcane (using a growth model developed for Florida sugarcane; Coale et al. 1993) and 2002 Texas field data for rice (Wilson et al., unpublished data). To correct for differences in sugarcane biomass between Louisiana and Florida, the estimated biomass given by the Florida model was multiplied by the ratio of the average sugarcane yield

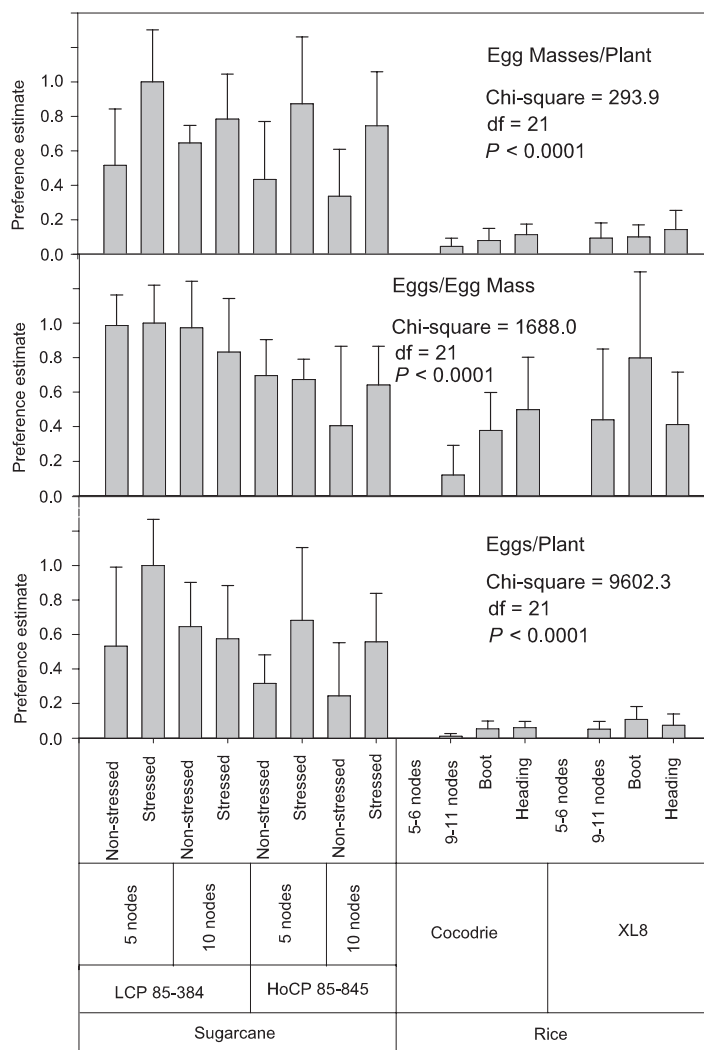


Fig. 1. Oviposition preference estimates ( $\pm$ SD) per plant from nonlinear regression models ranging from 0 (no oviposition) to 1 (maximum preference).

in Louisiana divided by the average sugarcane yield in Florida from 2000 to 2006 (81.2 tonnes/ha in Florida, 60.0 tonnes/ha in Louisiana; USDA-NASS). The predicted relative proportion of eggs laid on each of the two crops is presented for each region. This method assumes (1) the distribution of *E. loftini* moths in a region is neither biased toward rice nor sugarcane, (2) *E. loftini* moths respond similarly to all cultivars, and (3) the growth of Louisiana and East Texas sugarcane is similar to the growth of Florida sugarcane.

### Results

Over all seven datasets, egg masses ( $\chi^2 = 293.9$ ; df = 21;  $P < 0.0001$ ), eggs ( $\chi^2 = 9602.3$ ; df = 21;  $P < 0.0001$ ), and eggs per egg mass ( $\chi^2 = 1688.0$ ; df = 21;  $P < 0.0001$ ) per plant were significantly affected by host type. A total of 1,130 egg masses (mean =  $7.5 \pm 0.66$  [SE] egg masses per plant) and 29,337 eggs (mean =

$194 \pm 16.3$  eggs per plant) were laid in this study, corresponding to an average of  $29.1 \pm 1.6$  eggs per egg mass. Nonlinear regression models showed a strong fit between observed and predicted (equation 1 numbers of egg masses per plant ( $r^2 = 0.983$ ), eggs per egg mass ( $r^2 = 0.965$ ), and eggs per plant ( $r^2 = 0.967$ )). The preference coefficients (Fig. 1) showed values ranging from 1.0 (drought stressed sugarcane cultivar LCP 85-384 at the 5-node stage) to 0.0 (both rice cultivars at the 5–6 node tillering stage). Sugarcane was more attractive for oviposition than rice by 9.2-fold based on egg masses per plant, 2.3-fold based on eggs per egg mass, and 12.9-fold based on eggs per plant. Drought stress increased attractiveness by 1.8-fold based on egg masses and 1.6-fold based on eggs per plant. Egg masses per plant (1.2-fold), eggs per egg mass (1.6-fold), and eggs per plant (1.5-fold) were greater on cultivar LCP 85-384 than on cultivar HoCP 85-845. The young sugarcane (5 nodes) was more attractive



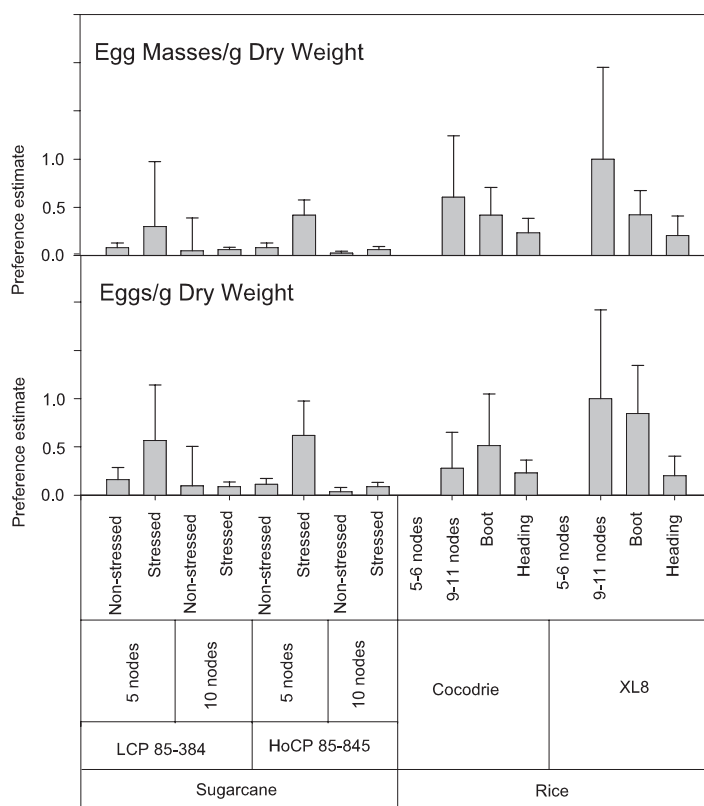


Fig. 2. Oviposition preference estimates ( $\pm$ SD) per gram of plant dry weight from nonlinear regression models ranging from 0 (no oviposition) to 1 (maximum preference).

than the old sugarcane (10 nodes) based on eggs per egg mass (1.2-fold) and eggs per plant (1.3-fold). On rice, cultivar XL8 was more attractive than Cocodrie by 1.4-fold based on egg masses per plant, 1.7-fold based on eggs per egg mass, and 1.9-fold based on eggs per plant. Preference estimates for egg masses per plant, eggs per egg mass, and eggs per plant increased with rice phenology on Cocodrie and for egg masses per plant on XL8. The boot stage was the most attractive for cultivar XL8 based on eggs per egg mass and eggs per plant. On sugarcane, 100% of the eggs were laid on dry leaves, dry tips of leaves, or dry leaf sheaths. On rice, 46% of the eggs were laid on dry leaves and 54% on green leaves, leaf sheaths, and on the stem.

Based on gram of plant dry weight, rice was 2.7-fold more attractive than sugarcane using egg masses and 1.7-fold using total eggs (Fig. 2). Averaging over both cultivars, drought stressed sugarcane at the five-node stage was 6.0-fold more attractive than all other sugarcane treatments based on egg masses per gram of plant dry weight and 6.2-fold based on total eggs.

Differences among the treatments were detected for a number of plant characteristics (Tables 2–5) and were associated with oviposition estimates based on egg masses per plant, eggs per egg mass, and eggs per plant (Table 6). On sugarcane, correlation analyses showed positive associations ( $P < 0.05$ ) between egg masses per plant and both essential FAAs (arginine,

Table 3. Multiple contrasts of plant measurements on rice and sugarcane from greenhouse oviposition test, Weslaco, TX, 2003–2004

	Contrasts ( <i>F</i> -values)				
	Dry weight <sup>a</sup>	Leaves <sup>b</sup>	Dry leaves <sup>b</sup>	Water potential (sugarcane only) <sup>c</sup>	Tillers (rice only) <sup>d</sup>
Rice versus sugarcane	2840.8 <sup>e</sup>	564.1 <sup>e</sup>	783.4 <sup>e</sup>	—	—
LCP 85–384 versus HoCP 85–845	7.71 <sup>f</sup>	6.33 <sup>f</sup>	35.53 <sup>f</sup>	6.09 <sup>e</sup>	—
Stressed sugarcane versus nonstressed	59.73 <sup>e</sup>	0.32 <sup>g</sup>	71.82 <sup>e</sup>	40.69 <sup>e</sup>	—
5- versus 10-node stage (sugarcane)	1318.21 <sup>e</sup>	56.06 <sup>e</sup>	24.56 <sup>e</sup>	0.83 <sup>g</sup>	—
Cocodrie versus XL8	0.50 <sup>g</sup>	30.70 <sup>e</sup>	0.00 <sup>g</sup>	—	43.82 <sup>e</sup>
Tillering versus boot and heading	3.00 <sup>g</sup>	124.95 <sup>e</sup>	10.94 <sup>e</sup>	—	26.23 <sup>e</sup>

<sup>a</sup> df = 1,68; <sup>b</sup> df = 1,96; <sup>c</sup> df = 1,24; <sup>d</sup> df = 1,56.

<sup>e</sup>  $P < 0.01$ ; <sup>f</sup>  $P < 0.05$ ; <sup>g</sup>  $P > 0.05$ .

Table 4. Free amino acid accumulations (nmol/10  $\mu$ l juice) in rice and sugarcane leaves from greenhouse oviposition test, Weslaco, TX, 2003–2004

	Sugarcane										Rice			
	LCP 85–384					HoCP 85–845					Boot		Heading	
	5 nodes		10 nodes		Stressed	5 nodes		10 nodes		Stressed	Cocodrie	XL8	Cocodrie	XL8
	Nonstressed	Stressed	Nonstressed	Stressed		Nonstressed	Stressed	Nonstressed	Stressed					
Alanine	1441.6a	1278.4a	172.7a	526.7a	447.0a	1238.2a	177.9a	801.8a	888.8a	1458.4a	1454.4a	489.2a	2.37	0.0251
Arginine	31.0b	59.4b	3.1b	48.7b	14.1b	41.6b	10.3b	90.9b	41.5b	286.9a	212.8a	86.1b	13.58	<0.0001
Aspartic acid	378.9cde	618.1bcde	174.9e	255.4de	252.3de	756.9bcd	161.3e	576.6	843.5bc	894.2b	1617.4a	591.2bcde	15.61	<0.0001
Glutamic acid	96.2d	329.1d	203.2d	386.7d	237.7d	634.8cd	249.3d	696.2bcd	217.9ab	3432.4a	3584.9a	2150.4abc	18.19	<0.0001
Glycine	0e	148.0bcde	104.3de	187.2bcd	42.9de	169.5bcde	131.6cde	310.0bc	12.64de	0e	599.8a	322.1b	22.45	<0.0001
Histidine	250.7bc	145.6c	87.4c	112.2c	91.8c	167.1bc	85.7c	126.3c	351.2bc	924.7a	492.5b	298.8bc	12.87	<0.0001
Isoleucine	9.4b	49.5b	0b	29.2b	12.3b	77.9b	35.2b	48.6b	43.8b	62.3b	350.4a	66.9b	21.09	<0.0001
Leucine	12.6c	37.9c	0c	84.5bc	23.5c	43.4c	5.2c	113.1bc	16.0c	36.7c	1069.2a	218.1b	102.9	<0.0001
Lysine	0b	12.1b	0b	10.2b	0b	12.4b	5.0b	29.5b	0b	0b	104.1a	21.5b	6.63	<0.0001
Methionine	3.8a	37.1a	0a	3.0a	0a	2.7a	0a	12.0a	1.4a	0a	19.0a	0a	1.15	0.3526
Phenylalanine	4.1b	42.4b	3.1b	38.7b	32.8b	62.5b	0b	58.9b	0b	39.3b	610.2a	102.0b	66.6	<0.0001
Proline	1679.5a	570.4a	125.8a	168.1a	458.9a	421.1a	153.4a	172.2a	1211.6a	1150.4a	0a	55.6a	2.04	0.0528
Serine	416.2c	281.7c	89.7c	182.8c	176.8c	218.4c	134.6c	253.7c	1025.0b	1931.9a	1366.3b	513.1c	35.73	<0.0001
Threonine	176.1bc	170.1bc	30.6c	88.6c	42.1c	163.3bc	28.9c	142.6bc	287.5abc	393.1ab	537.3a	209.3bc	8.26	<0.0001
Tyrosine	18.0b	168.1b	96.8b	94.9b	144.3b	273.1b	199.5b	141.6b	0b	8.66b	839.7a	180.1b	18.9	<0.0001
Valine	124.9bc	86.0c	35.6c	18.4c	56.4c	84.9c	62.4c	0c	89.3c	232.8ab	339.5a	93.0c	12.43	<0.0001
Total	4642.8cd	4033.9cd	1127.2d	2196.7cd	2032.9cd	4675.1cd	1440.4d	3960.1cd	6930.0bc	10852.3ab	13197.4a	5397.4cd	13.84	<0.0001
Sum <sup>b</sup>	612.4cd	640.2cd	232.8d	622.0cd	273.0cd	709.9cd	159.8d	433.7cd	830.8cd	1975.7b	3735.0a	1095.7c	33.9	<0.0001

Means within the same row followed by the same letter are not significantly different ( $P < 0.05$ ; Tukey's [1953] HSD).<sup>a</sup> df = 11,36.<sup>b</sup> Sum of concentrations of arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, and valine.

**Table 5.** Multiple contrasts of free amino acid accumulations (nmol/10  $\mu$ l juice) in rice and sugarcane leaves from greenhouse oviposition test, Weslaco, TX, 2003–2004

	Contrasts ( <i>F</i> -values)					
	Rice versus sugarcane <sup>a</sup>	LCP 85–384 versus HoCP 85–845 <sup>a</sup>	Stressed sugarcane versus nonstressed <sup>a</sup>	5- versus 10-node stage (sugarcane)	Cocodrie versus XLS <sup>a</sup>	Boot versus heading <sup>a</sup>
Alanine	2.90 <sup>e</sup>	1.02 <sup>e</sup>	2.61 <sup>e</sup>	8.19 <sup>e</sup>	0.39 <sup>e</sup>	0.40 <sup>e</sup>
Arginine	68.95 <sup>d</sup>	0.05 <sup>e</sup>	7.52 <sup>e</sup>	0.01 <sup>e</sup>	6.39 <sup>e</sup>	0.40 <sup>e</sup>
Aspartic acid	85.30 <sup>d</sup>	1.18 <sup>e</sup>	17.65 <sup>e</sup>	8.07 <sup>e</sup>	21.83 <sup>d</sup>	5.08 <sup>e</sup>
Glutamic acid	171.5 <sup>d</sup>	1.94 <sup>e</sup>	3.72 <sup>e</sup>	0.53 <sup>e</sup>	0.04 <sup>e</sup>	0.09 <sup>e</sup>
Glycine	18.60 <sup>d</sup>	4.27 <sup>e</sup>	26.65 <sup>d</sup>	12.9 <sup>d</sup>	15.63 <sup>d</sup>	153.4 <sup>d</sup>
Histidine	84.70 <sup>d</sup>	0.42 <sup>e</sup>	0.03 <sup>e</sup>	1.61 <sup>e</sup>	7.79 <sup>e</sup>	12.68 <sup>d</sup>
Isoleucine	64.42 <sup>d</sup>	1.78 <sup>e</sup>	5.89 <sup>e</sup>	0.21 <sup>e</sup>	43.02 <sup>d</sup>	59.28 <sup>d</sup>
Leucine	267.1 <sup>d</sup>	0.29 <sup>e</sup>	7.73 <sup>e</sup>	1.18 <sup>e</sup>	197.6 <sup>e</sup>	436.8 <sup>d</sup>
Lysine	10.83 <sup>d</sup>	0.51 <sup>e</sup>	3.21 <sup>e</sup>	0.46 <sup>e</sup>	13.19 <sup>d</sup>	30.43 <sup>d</sup>
Methionine	0.11 <sup>e</sup>	0.99 <sup>e</sup>	2.92 <sup>e</sup>	0.90 <sup>e</sup>	0.95 <sup>e</sup>	0.70 <sup>e</sup>
Phenylalanine	156.3 <sup>d</sup>	0.95 <sup>e</sup>	6.99 <sup>e</sup>	0.32 <sup>e</sup>	128.3 <sup>d</sup>	264.1 <sup>d</sup>
Proline	0.37 <sup>e</sup>	1.66 <sup>e</sup>	1.11 <sup>e</sup>	5.19 <sup>e</sup>	0.00 <sup>e</sup>	9.14 <sup>e</sup>
Serine	274.4 <sup>d</sup>	0.29 <sup>e</sup>	0.08 <sup>e</sup>	2.88 <sup>e</sup>	0.07 <sup>e</sup>	30.19 <sup>d</sup>
Threonine	59.19 <sup>d</sup>	0.34 <sup>e</sup>	3.61 <sup>e</sup>	2.99 <sup>e</sup>	4.34 <sup>e</sup>	0.38 <sup>e</sup>
Tyrosine	14.51 <sup>d</sup>	5.74 <sup>e</sup>	1.63 <sup>e</sup>	0.06 <sup>e</sup>	40.48 <sup>d</sup>	97.64 <sup>d</sup>
Valine	62.52 <sup>d</sup>	0.88 <sup>e</sup>	1.72 <sup>e</sup>	8.60 <sup>e</sup>	3.60 <sup>e</sup>	4.13 <sup>e</sup>
Total	101.7 <sup>d</sup>	2.28 <sup>e</sup>	2.73 <sup>e</sup>	4.07 <sup>e</sup>	3.73 <sup>e</sup>	0.16 <sup>e</sup>
Sum <sup>b</sup>	190.4 <sup>d</sup>	0.04 <sup>e</sup>	4.51 <sup>e</sup>	2.04 <sup>e</sup>	18.70 <sup>d</sup>	34.31 <sup>d</sup>

<sup>a</sup> df = 36.<sup>b</sup> df = 1,36.<sup>c</sup>  $P < 0.05$ ; <sup>d</sup>  $P < 0.001$ ; <sup>e</sup>  $P > 0.05$ .

phenylalanine, and threonine) and dry leaves and between eggs per plant and both essential FAAs (methionine and threonine) and dry leaves (Table 6). On rice, correlation analyses showed positive associations ( $P < 0.05$ ) between egg masses per plant and both essential FAAs (threonine and valine) and dry leaves, between eggs per egg mass and both dry leaves and tillers, and between eggs per plant and the essential FAA alanine, dry leaves, and tillers (Table 6). Multiple linear regression analyses with the sugarcane data showed that egg masses per plant were positively associated with dry leaves (parameter estimate = 0.0818) and methionine (0.00519) and negatively as-

sociated with total leaves per plant ( $-0.0707$ ;  $F = 44.5$ ;  $df = 4, 3$ ;  $P = 0.0005$ ;  $r^2 = 0.97$ ). Eggs per egg mass showed a positive association with dry leaves (0.0659) and alanine (0.00112) and a negative association with the sum of essential FAAs ( $-0.00245$ ;  $F = 7.5$ ;  $df = 4, 3$ ;  $P = 0.064$ ;  $r^2 = 0.85$ ). Eggs per plant were positively associated with dry leaves (0.0199), aspartic acid (0.000338), and methionine (0.0105;  $F = 15.6$ ;  $df = 4, 3$ ;  $P = 0.0239$ ;  $r^2 = 0.92$ ). On rice, the preference coefficients were not significantly associated with any of the plant-based estimates using regression analyses ( $P \geq 0.05$ ); however, strong trends were observed, with egg masses per plant positively associated with

**Table 6.** Correlation coefficients ( $P < 0.1$ ) of *E. loftini* oviposition estimates with plant phenology and physiochemical measurements

Preference estimates	Sugarcane				Rice			
	Plant variable	<i>n</i>	<i>r</i>	<i>P</i>	Plant variable	<i>n</i>	<i>r</i>	<i>P</i>
Egg masses/plant	Dry leaves	12	0.740	0.0059	Dry leaves	16	0.809	0.0001
	Arginine	8	0.823	0.0122	Threonine	4	0.988	0.0125
	Phenylalanine	8	0.821	0.0125	Aspartic acid	4	0.982	0.0176
	Aspartic acid	8	0.796	0.0181	Essential FAAs	4	0.971	0.0287
	Essential FAAs	8	0.776	0.0236	Valine	4	0.963	0.0372
	Water potential	8	0.750	0.0322	Total FAAs	4	0.954	0.0461
	Threonine	8	0.730	0.0399	Dry weight	16	0.470	0.0662
	Methionine	8	0.706	0.0503	Methionine	4	0.915	0.0852
	Isoleucine	8	0.690	0.0585				
	Lysine	8	0.689	0.0587				
	Leucine	8	0.647	0.0827				
Eggs/egg mass					Dry leaves	16	0.732	0.0013
					Tillers	16	0.506	0.0456
					Total leaves	16	0.456	0.0740
Eggs/plant	Methionine	8	0.850	0.0076	Dry leaves	16	0.758	0.0007
	Threonine	8	0.763	0.0277	Alanine	4	0.985	0.0149
	Dry leaves	12	0.626	0.0294	Glutamic acid	4	0.963	0.0374
	Essential FAAs	8	0.749	0.0325	Tillers	16	0.515	0.0414
	Aspartic acid	8	0.739	0.0403	Serine	4	0.936	0.0639
	Arginine	8	0.709	0.0492	Total FAAs	4	0.936	0.0640
	Alanine	8	0.689	0.0587	Arginine	4	0.919	0.0815
	Water potential	8	0.662	0.0737	Total leaves	16	0.442	0.0862



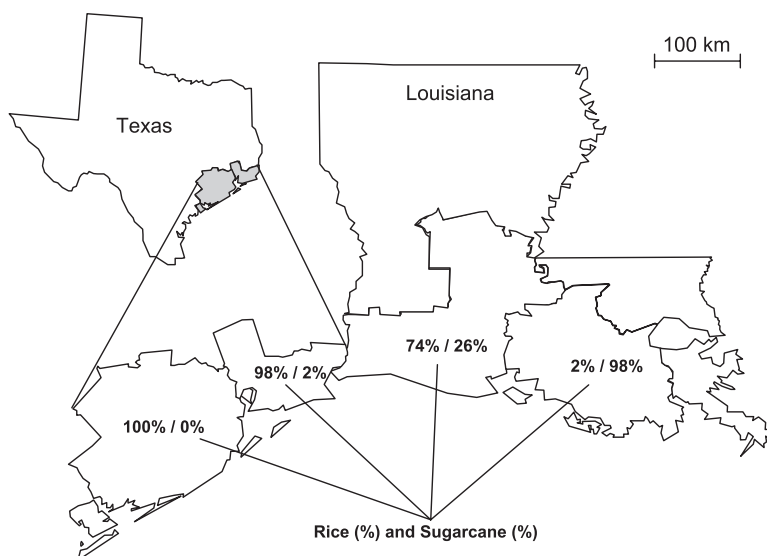


Fig. 3. Relative availability of rice and sugarcane for oviposition by *E. loftini* across Texas and Louisiana in 2004.

threonine (0.000783;  $F = 79.0$ ;  $df = 2,1$ ;  $P = 0.079$ ;  $r^2 = 0.97$ ).

During 2004, sugarcane and rice production was 0 and 73,936 ha west of Houston, 405 and 18,836 ha east of Houston in the Texas upper gulf coast region, 58,903 and 168,396 ha in southwest Louisiana, and 76,057 and 2,187 ha in southcentral Louisiana, respectively (Fig. 3). Biomass estimates for sugarcane and rice were 2.0 and 0.12 t/ha on 1 May, 2.7 and 0.81 t/ha on 15 May, 4.9 and 7.3 t/ha on 15 June, and 7.1 and 9.3 t/ha on 6 July, respectively. The predicted relative oviposition pattern by *E. loftini* on sugarcane and rice in each of the four regions is presented in Fig. 4. These results only consider egg laying on sugarcane and rice and do not consider oviposition on other hosts. On 1 May, in areas where sugarcane is available, this crop is projected to receive 100% of the eggs, because rice is not a host during early stages of development (Fig. 4B–D). On 15 May, rice is more attractive than sugarcane on a biomass basis; however, sugarcane is predicted to receive a disproportionate amount of eggs, as a result of its greater mass in all areas where sugarcane is grown. On 15 June and 6 July, rice is more attractive than sugarcane, and the proportion of the eggs on rice will approach an average of 4.7% in southeast Louisiana, where rice represents only 2% of the combined area of these two crops.

### Discussion

**Oviposition on Sugarcane.** Eggs on sugarcane were laid exclusively on dry leaves, dry tips of leaves, and dry leaf sheaths. Eggs have been observed on sugarcane in the field between the leaf sheath and the stalk (Van Zwaluwenberg 1926, Flanders 1930) and on dead leaves (Van Leerdaam et al. 1984). Van Leerdaam et al. (1986) conducted a greenhouse bioassay and found that 99% of *E. loftini* oviposition occurred in concealed

sites on dried sugarcane leaves located on the lower part of the plant (i.e., between soil surface and 80 cm height). Our results similarly showed a significant correlation between oviposition and dry leaves on sugarcane, with all eggs laid on dry leaves or dry tips of leaves. The numbers of eggs laid and the number of dry leaves per sugarcane plant increased under drought stressed conditions. Reay-Jones et al. (2005a) showed that both *E. loftini* injury and production of moths on sugarcane can be reduced by irrigation. Preference for drought stressed sugarcane provides a mechanism that partially explains the breakdown of plant resistance observed in the field.

Insecticide studies (Meagher et al. 1994, Legaspi et al. 1999a, b) and extensive attempts at classical biological control (Meagher et al. 1998) have not resulted in effective *E. loftini* control programs. Oviposition of *E. loftini* in concealed sites on dried sugarcane leaves on the lower portion of the plant might be a mechanism to protect eggs from predation, parasitism (Van Leerdaam et al. 1986), and insecticides.

On a per plant basis, sugarcane cultivar LCP 85–384 was more attractive for oviposition than HoCP 85–845. Greenhouse and laboratory studies have previously shown only slight differences in *E. loftini* oviposition among sugarcane cultivars, whereas differences in larval establishment indicated antibiosis as a more important resistance mechanism (Meagher et al. 1996). A field study has shown that sugarcane cultivar LCP 85–384 was more susceptible to *E. loftini* than HoCP 85–845 based on both percentage of bored internodes and moth emergence per hectare (Reay-Jones et al. 2003). Cultivar LCP 85–384 had more dry leaves than HoCP 85–845 in our study, which seemed to affect oviposition preference. The decreased oviposition on HoCP 85–845 therefore is an antixenosis mechanism conferring resistance to *E. loftini*.

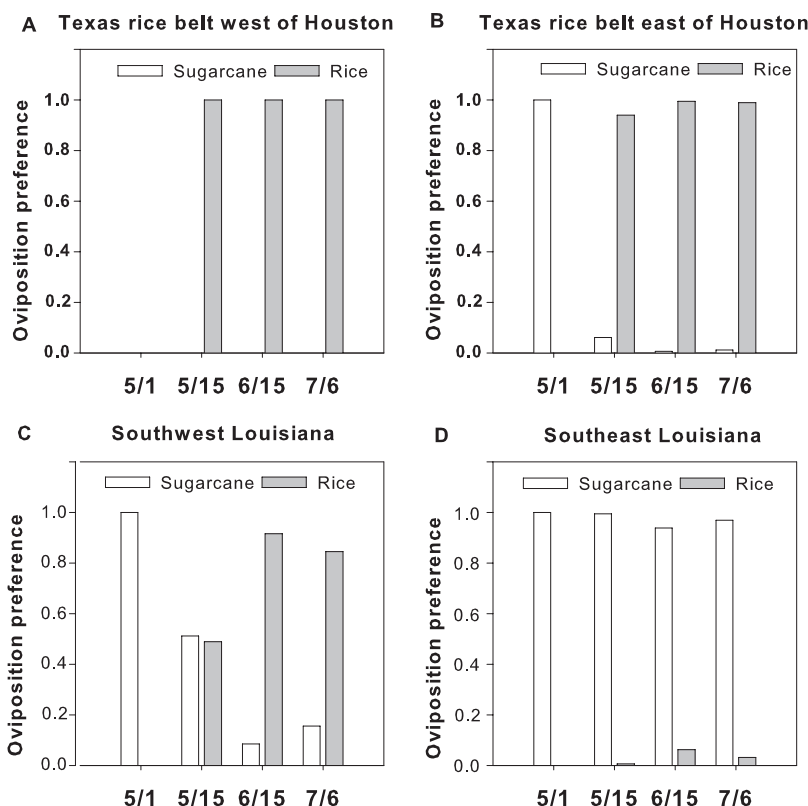


Fig. 4. Potential *E. loftini* oviposition patterns based on eggs per plant dry weight in (A) the Texas rice belt west of Houston (100% rice), (B) Texas rice belt east of Houston (98% rice, 2% sugarcane), (C) southwest Louisiana (74% rice, 26% sugarcane), and (D) southeast Louisiana (2% rice, 98% sugarcane).

**Oviposition on Rice.** *Eoreuma loftini* eggs were distributed on rice green leaves, leaf sheaths, stems, and dry leaves. Oviposition did not occur in sites as cryptic as on sugarcane, indicating potential increased exposure in the field to mortality factors such as parasitoids, predators, and insecticides. The relative concealment of eggs on sugarcane might explain the preference over rice based on oviposition on a per plant basis. The tillering stages were not as attractive as either the boot or heading stages, possibly because of a reduced number of oviposition sites (i.e., green and dry leaves) on young rice plants. The pest status of *E. loftini* on rice in the Texas Rice Belt is increasing as the insect spreads. Field insecticide trials on rice have shown yield losses as much as 50% or greater attributable to stem borers [*E. loftini* and *Diatraea saccharalis* (F.)] (Reay-Jones et al. 2005b). Insecticidal control is more effective on rice than on sugarcane, likely because of increased egg and larval exposure.

**Drought Stress Effects on Sugarcane Physiology.** Drought stress significantly increased water potential and levels of several FAAs (arginine, aspartic acid, glycine, leucine, phenylalanine) in sugarcane; however, effects were not detected for free proline, which has previously been shown to be an indicator of water deficit stress (Reay-Jones et al. 2005a, Showler 2002). Discontinuance of daily watering of sugarcane in

greenhouse pots for 12 d increased levels of proline by 2.5-fold (Muqing and Ru-Kai 1998). Other types of stress have also increased levels of free proline in sugarcane leaves 1.6-fold (salt stress) (Joshi and Naik 1980), 6.2-fold (*Colletotrichum falcatum* Went infection) (Singh et al. 1993), and 1.2-fold (iron chlorosis) (Jain and Shrivastava 1998). When plants are subject to dehydration, osmoregulation is achieved by accumulation of free proline (Heuer 1994). Free proline levels also have been shown to increase under drought stress in sugar beets, *Beta vulgaris* L., by 12-fold (Gzik 1996) and in cotton, *Gossypium hirsutum* L., by 58-fold (Showler and Moran 2003). Free proline seems to be the most widespread and consistent amino acid related to drought stress (Aspinall and Paleg 1981). In our study, reducing irrigation 2 wk before the beginning of the experiment might not have been sufficient to elicit an accumulation of proline, even though other stress symptoms, such as increased frequency of dry leaves, were visible.

**Mechanisms of Oviposition Preference.** The majority of nitrogen is acquired by insects through absorption in the gut (Brodbeck and Strong 1987). Increased levels of FAAs under plant-stressed conditions can increase insect herbivore populations (White 1984). Three potential physiological mechanisms may explain the enhanced nutritional quality of plants under

stress: (1) FAAs are nutritionally superior to proteins, (2) FAAs are more readily available than proteins because of the absence of any proteinase inhibitors, and (3) FAAs are physically more accessible because of increased solubility (Cockfield 1988). Certain amino acids are known to be essential for insect development (Vanderzant 1958, Nation 2002). Artificial diets with amino acid distributions simulating anthers were adequate for survival and development of the tobacco budworm, *Heliothis virescens* (F.) (Hedin et al. 1991). Moths possess contact chemoreceptors on antennae, proboscis, tarsi, and ovipositors, which assist in accepting or rejecting a host plant based on presence or absence of secondary or primary compounds (Städler 1984). FAAs can elicit electrophysiological responses of the sensilla of the adult tobacco budworm, the corn earworm, *Heliothis armigera* (Hübner), and *Spodoptera littoralis* (Boisduval) (Blaney and Simmonds 1988). Oviposition of the beet armyworm was increased on cotton under drought stress, which was correlated with greater levels of essential FAAs (Showler and Moran 2003). Assuming that *E. loftini* can detect host plant FAA levels and that such levels influence oviposition preference, levels of essential FAAs may help explain the observed variability in egg laying.

Insects often oviposit on plants that maximize their survival and development (Showler 2001). Nonpublished greenhouse studies by M. Sétamou and A. T. Showler, mentioned in Reay-Jones et al. (2003), have indicated that survival and development of *E. loftini* on sugarcane is enhanced within a certain range of drought stress. Our study showed increased attractiveness of drought-stressed sugarcane for oviposition. A positive correlation may exist between preference and performance on sugarcane. However, performance, as measured by the rate of population increase, of *E. loftini* on rice has not been studied. Reay-Jones et al. (2005b) has shown that cultivar XL8, despite being more attractive for oviposition in our study, was more resistant to stem borers than Cocodrie. Poor relationships between ovipositional preference and performance can be explained by several hypotheses (Thompson 1988). Further studies are necessary to determine which hypothesis best explains the relationship between performance and preference of *E. loftini*.

Host plant selection by moths and butterflies can be viewed as a sequence of behavioral events consisting of (1) searching, orientation, and encounter, (2) landing and contact evaluation, and (3) acceptance or rejection (Renwick and Chew 1994). Alighting on a potential host plant is the result of integrating information perceived by the moth, which includes visual, olfactory, gustatory, and mechanical cues (Ramaswamy 1988). Contact chemoreception is the most predominant sensory modality involved in host acceptance (Ramaswamy 1988). Host location and acceptance in oviposition preference studies are reflected by number of egg masses per plant. The size of each egg mass might reflect the moth's perception of host plant suitability. Smaller egg masses may occur on

plants that are perceived as having low suitability. Moths may assess host acceptability and host suitability using different mechanisms, which likely involve different host cues. Our analyses yielded associations between several plant characteristics and the different oviposition parameter estimates (Table 6), which might reflect such behavioral steps.

On a plant selection basis, drought-stressed sugarcane cultivar LCP 85-384 (five nodes) was the most attractive for oviposition based on egg masses laid. Once a female began egg laying on sugarcane, its attraction was even more apparent as indicated by the 2.3-fold greater numbers of eggs per egg mass when contrasting with the number of eggs per egg mass placed on rice. From a behavioral perspective, these results suggest this species is able to regulate its egg deployment strategy to account for the size of the plant host and therefore the available sites for larval feeding. Rice plants are much smaller than sugarcane plants and large egg masses on rice would require greater dispersal of larvae, thus exposing them to a greater degree of mortality. The larger number of egg masses and egg mass size on sugarcane indicates that this plant is not only preferred for host location and acceptance, but is also perceived as the most suitable plant by *E. loftini*. In our study, oviposition on sugarcane was associated with arginine (egg masses per plant) and aspartic acid (eggs laid per plant), which both increased under stress. Reducing plant stress with irrigation might assist in decreasing *E. loftini* oviposition in sugarcane by decreasing both the nutritional value of the crop for this insect and the number of ovipositional sites (i.e., dry leaves). Young sugarcane (5 nodes), despite having fewer dry leaves than old sugarcane (10 nodes), was more attractive for egg-laying, which may have been caused by the higher levels of several FAAs essential for insect development (alanine and valine). On rice, associations were established between egg masses per plant and essential FAAs (threonine and valine) and dry leaves. Rice cultivar XL8, which was more attractive for oviposition compared with Cocodrie, had higher levels of the essential FAA histidine. The greater resistance of cultivar XL8 compared with Cocodrie in the field (Reay-Jones et al. 2005b) might be caused by other biochemical and physiological factors that have been shown to influence the resistance of rice to stem borers (Chaudhary et al. 1984, Heinrichs 1994). Cultivar XL8 also had more tillers, a plant trait that was positively associated with egg masses per plant. *E. loftini* laid more eggs on rice plants of large biomass, a common response in oviposition behavior among other insects (Asman 2002, Vasconcellosneto and Monteiro 1993).

Our study suggests that host plant foliar FFAs may affect the oviposition preference of *E. loftini*. Plant volatiles can have a major role in lepidopteran oviposition (Renwick and Chew 1994), but have not yet been identified for *E. loftini*. Foliage weight has been correlated with the emission of volatiles from potato plants, *Solanum tuberosum* L. (Agelopoulos et al. 1999). If the oviposition of *E. loftini* is greatly affected by the emission of plant volatiles that varies with plant

size, the estimation of preference on a dry weight basis might better quantify host plant selection than on a per plant basis. In addition to the quantity of volatiles emitted from a plant, moth oviposition can be affected by the quality of volatiles emitted, such as the ratio of several compounds (Thompson and Pellmyr 1991). Determining preference on a plant basis might therefore better quantify host choice in *E. loftini* if quality of plant volatile emission is a more important factor than quantity.

**Simulated Oviposition Patterns.** Our study indicates that rice is more attractive than sugarcane on a biomass basis. However, the projected potential oviposition patterns of *E. loftini* might vary greatly with the biomass of the available host plants (Fig. 4). Sugarcane plants develop biomass more quickly in the spring than rice and are expected to receive a greater proportion of eggs earlier in the season. In areas where rice is the dominant crop (Fig. 4B), rice might overwhelmingly receive the greatest proportion of eggs as its biomass increases. As the proportion of sugarcane increases (Fig. 4B and C), oviposition is expected to increase on sugarcane. When sugarcane is the dominant crop (98% of the production area; Fig. 4D), oviposition might still occur at relatively high rates on rice (3.5% on 6/15) because of increased attractiveness of the biomass of rice compared with sugarcane.

Our initial assumptions made to determine these oviposition patterns imply a somewhat simplified agroecosystem. *E. loftini* can develop on numerous plant species (Reay-Jones 2005), and the role of alternate hosts in the population dynamics of the insect is currently being studied. Spatial dispersal patterns of *E. loftini* between crop hosts have also not been studied. Also, the growth model for sugarcane used in our study was developed in Florida, where conditions can be different from Louisiana (i.e., a shorter growing season in Louisiana than in Florida). To correct for this, we assumed a similar relationship between the two states for both sugarcane yield and dry weight. Our predictions provide insight into how *E. loftini* might distribute its populations between sugarcane and rice as infestations move into Louisiana. However, data from field studies on the oviposition behavior of *E. loftini* are also needed to verify the validity of the results reported here from greenhouse studies.

Early-instar *E. loftini* larvae have limited mobility and must feed on or very near the plant on which the eggs are laid. Levels of antixenosis can help control pests of crops in some integrated pest management (IPM) systems (Smith 1989) and might assist in developing a defense strategy against *E. loftini*. Resistant sugarcane cultivar HoCP 85–845, which has a reduced number of dry leaves, is less attractive than susceptible LCP 85–384. Leaf FAA levels varied with host species, cultivar, stress, and phenology and were associated with oviposition preference estimates using both correlation and regression analyses. Reducing drought stress decreases both host plant suitability and attractiveness for oviposition. Because sugarcane is more attractive than rice, populations from rice fields will be expected to contribute to enhancing infestations on

proximate sugarcane in some areas in Louisiana and Texas. On rice, cultivar XL8 has been shown to be more resistant to stem borers than Cocodrie, despite being more attractive for oviposition (Reay-Jones et al. 2005b). The use of this resistant rice cultivar as a trap crop within the rice agroecosystem might be effective in reducing infestations on proximate host crops if the resistance mechanisms are antibiotic. Our study has shown substantial differences in *E. loftini* oviposition among host plants and the preference was associated with several host plant characteristics. Understanding the population dynamics on both sugarcane and rice is necessary to conceptualize areawide management strategies.

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